CHAPTER 7

The evolution of dual-function signals

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Abstract

The evolution of ornaments has been studied extensively in the contexts of male-male competition and female choice. A single ornament can however be used in both contexts, and such 'dual-function' signals have been frequently found to occur in nature. The aim of this study is to develop a theoretical framework in order to investigate the occurrence and evolutionary implications of dual-function signalling. We consider a dynamical model where signalling may evolve in the context of male-male competition where males may differ in their fighting capabilities and in the context of female choice in situations where males vary in their ability to provide direct benefits. We find that ornaments can be used in both contexts simultaneously. Furthermore we show that the use of an ornament in one context can facilitate its use in another context, in other words, an ornament used in male-male competition can pave the way for female choice for ornamented males and vice versa. Dual-function signalling does affect the equilibria attained in comparison to single function contexts. Analysing complex signalling system like attempted here is not a trivial task and several restricting assumptions had to be made. Nevertheless, we belief this is a fruitful approach which can provide new insights in processes that were previously too complex to analyse.

Introduction

The use of signals in animal communication is widespread in nature and is evident in many different contexts (Maynard Smith and Harper 2003). Central to signalling is the transfer of information from a 'sender' to a 'receiver' who might choose to adapt its behaviour accordingly. Signals are frequently used in sexual selection and may function in male-male competition or female choice (e.g. Andersson 1994). The evolution of signalling is not trivial, as the evolutionary interests of the sender and receiver are often not the same. To illustrate this, consider a situation where males with different fighting abilities (or 'resource holding potential'; Parker 1974) compete over a resource and where engaging in an escalated fight is costly. Males with high fighting abilities could reduce the costs of fighting by signalling their quality to their opponents. If an opponent is of low quality, it should retreat. However, once such a signalling convention is adopted, it might pay for a male with low fighting capabilities to 'cheat', i.e. to use the same signal and thereby increasing its chances of getting the resource without an escalated fight. Similarly, for a female it would be beneficial to be able to single out males with high parental ability, since this would increase her reproductive success. Accordingly, it is in the interest of the high-quality males to signal their parental ability, since this would increase their mating chances. However, low-quality males could also benefit from producing the same signal which will result in a reduction of information content of the signal.

Several types of signals are robust against cheating, allowing for reliable signalling to persist (Maynard Smith and Harper 2003; Hurd and Enquist 2005). Indices, for example, are signals that simply cannot be faked. An index (e.g., body weight) thus necessarily indicates the quality of an individual with high reliability. Alternatively, the sender and receiver may have some joint interests, for example avoiding escalated fights, which prevent individuals from cheating (Maynard Smith and Parker 1976; Eshel and Sansone 2001; Maynard Smith and Harper 2003). The badge-of-status is a well-known example of such a convention (Krebs and Dawkins 1984). A third mechanism that allows for evolutionarily stable, honest signalling is the handicap principle (Zahavi 1975; Grafen 1990). A signal is a handicap if the cost of signal production depends on the individual's quality, so that low-quality individuals have no or reduced ornament expression.

Traditionally, the evolution of signalling has been investigated separately in the contexts of female choice and male-male competition (Andersson 1994). Substantial empirical evidence for female preference for 'handicap' ornaments has lead to the common wisdom that female choice is based on costly traits (such as carotenoid-based feather ornaments; Olson and Owens 1998). In contrast, research on signalling in male-male competition has predominantly

focused on conventional signals, which can be very cheap to produce (e.g. melanin based ornaments; Badyaev and Hill 2000). Whether there is indeed a dichotomy in the cost and function of signals used in inter- versus intra-sexual selection has been questioned (e.g. Maynard Smith 1994). For example, for feather pigmentations it was found that carotenoids might not be as costly as previously assumed (Jawor and Breitwisch 2003; Griffith et al. 2006). Another argument against a mechanistic link between cost and function comes from the observation that in nature, the same ornaments is frequently used in both male-male competition and female choice. Examples of such dual-function signals are the red belly of stickleback (Candolin 2000), the black facial mask of the common yellowthroat (Tarof et al. 2005) and the eye span of the stalk-eyed fly (Cotton et al. 2004 and references therein).

The idea that signals can have a function in both sexual selection contexts is not new (Kodric-Brown and Brown 1984; Andersson 1994) and has considerable empirical support (see Berglund et al. 1996 and references therein). Interactions between female choice and male-male competition may have important evolutionary implications, for example, when speciation is driven by sexual selection (Seehausen and Schluter 2004; van Doorn et al. 2004). There has been an increased awareness and interest among empiricists in dual-function signals (e.g. Candolin 2000; Wong and Candolin 2005; Griggio et al. 2007).

The theoretical interest in this topic has been limited. We are only aware of a single theoretical study that addressed this problem under highly simplifying assumptions (Johnstone and Norris 1993). The lack of a good theoretical understanding of dual-function signalling is not surprising, as male-male competition itself is complex and difficult to fully comprehend. Combining this with female choice increases the difficulties even further. Still we think that an attempt to integrate both contexts has to be made. This paper is a first step in this direction. It is well conceivable that interactions between inter- and intra-sexual selection change signal evolution and lead to fundamentally different predictions compared to a situation where such interactions are absent.

The issue of dual-function signalling presents a number of interesting questions. The first one relates to the establishment of new signals. The evolution of a new signal is not trivial, and may require special conditions, such as a sensory bias in the receiver of the signal. Signal evolution might be less problematic if the signal is used in another context and therefore already present in the population. Second, conventional signals in male-male competition are cheap to produce, but will such conventional signalling system remain stable when expressing the signal provides an additional benefit in a different context (e.g. increased mating chance)? Third, and more generally, should one expect that signals used in one context become integrated in another context, or should one rather expect the evolution of separate signals for different contexts?

The aim of this study is to develop a dynamical model incorporating male-male competition and female choice with the possibility to study both processes in isolation and in concert. Male-male competition is based on an asymmetrical Hawk-Dove game played in a population of individuals with different fighting abilities. Female choice may evolve as a consequence of differences in parental ability between the males. Males may invest in an ornament to signal their abilities. We will first describe male-male competition and female choice separately. Importantly, the model structure we use allows for reciprocal interaction between the two processes. This opens up the possibility for a signal with a single function to attain a dual function, i.e., a signalling function in both male-male competition and female choice. However, due to the inherent complexity of such a complex signalling model, we have to make several simplifying assumptions. For example, our model currently incorporates phenotypic quality differences but no heritable variation in quality as in good-genes models. The first aim of this study is to find out if signals with a combined function can arise. Second, to what extent do male-male competition and female choice work synergistically? Does female choice facilitate or hamper the use of signals in male-male competition? Lastly, does a dual function have an effect on signal-dependent behaviour in each of the two contexts? Do males play other condition-dependent strategies if signals have a dual function?

Model overview

Quality differences and ornamentation

We are interested in the evolution of signals that are used in different contexts, in this case male-male competition and female choice. We ask ourselves whether reliable signals can evolve either for fighting ability in male-male competition or parental ability in the context of female choice. For simplicity we assume that the differences in male 'qualities' (i.e. fighting ability and/or parental ability) are not heritable and assigned at random. Accordingly, we do not address indirect benefits of signalling systems that are related to heritable quality differences. Each male is faced with the decision whether or not to invest in an ornament. Ornament investment is costly and can, for simplicity, not be made dependent on the male's quality. One might think of a system where investment decisions are made before quality differences arise. Whether investment results in the expression of the ornament depends on the quality of the male: the probability that an ornament is actually expressed is higher for a high quality male. In a single function context, ornament expression is dependent on either fighting or parental ability. In a dual-function context, an individual's 'overall' quality is determined by the combined effect of both fighting and parental ability.

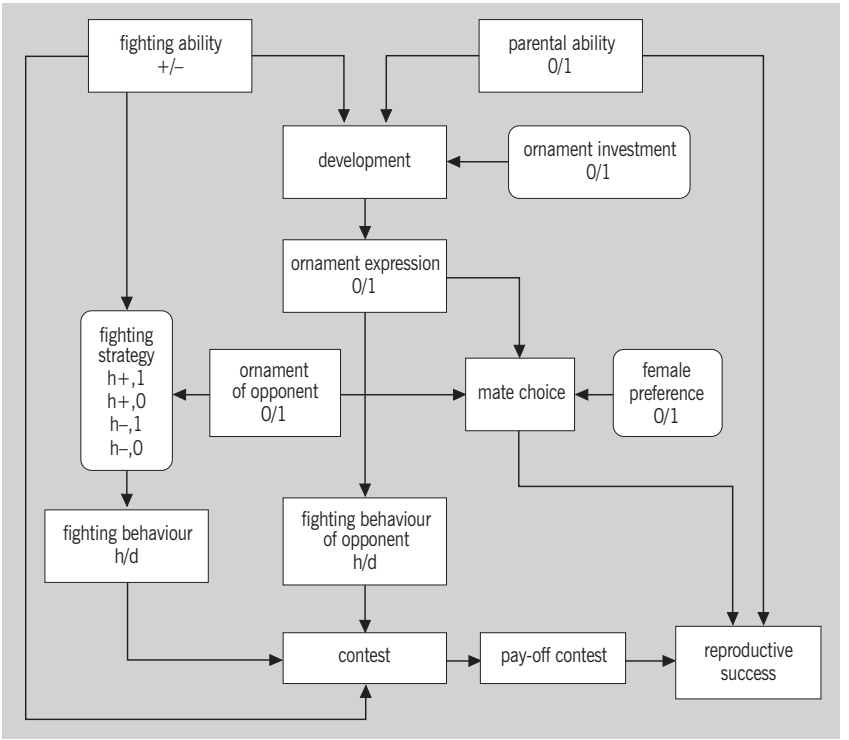

Figure 7.1. A schematic representation of the model.

We will discuss these assumptions in more detail later on. Figure 7.1 provides an overview of the model structure. We will now continue to briefly introduce the different parts of the model (male-male competition, female choice and both combined). A more detailed explanation will be given when the results of these models are presented.

Male-male competition

Each male is involved in a single contest, which is modelled by an asymmetrical Hawk-Dove game where the players differ in fighting ability (e.g. Maynard Smith and Price 1973; Maynard Smith and Parker 1976; Hammerstein 1981). It is well known that external cues can and should be used to settle a contest, since such cues allow the avoidance of escalated conflicts. The question we pose is whether such cues (i.e. ornaments) will evolve from scratch if they are costly to produce. Every individual knows his own fighting ability, but not that of his opponent. Accordingly, strategic decisions with respect to the conflict can only

be based on one's own fighting quality and whether or not the opponent has an ornament. For simplicity we neglect the possibility that an individual can also adjust its strategy on whether or not he actually expresses the ornament. Whether or not the opponent expresses the ornament is informative with respect to the expected outcome of an escalated conflict, since the ornament is assumed to be a revealing handicap. Each male can decide to invest in the ornament, but this will come at a cost (reduced viability). Among the individuals that chose to invest in the ornament, individuals with low fighting capability express the ornament with a lower probability than high-quality individuals. One could easily imagine such a condition-dependent ornament to serve as a signal, and one would expect an individual with low fighting capabilities to be more reluctant to escalate and fight when faced with an ornamented opponent, since such an opponent is likely to have high fighting capabilities. In a first step we want to address the question if males will invest in such costly ornaments and make their strategy dependent on it.

Female choice

Each female samples two males and is more likely to mate with the more attractive one of them (best-of-two; Bulmer 1989). The males differ in their ability to provide direct benefits, i.e. mating with a high quality male will increase the reproductive success of a female (e.g. Hoelzer 1989). Males can invest in a costly ornament and ornament expression is condition dependent such that males with low parental ability have a lower probability of expressing the ornament. The question is whether and under which circumstances females will express a costly preference for ornamented males, and whether males will invest in ornament expression.

Interaction between male-male competition and female choice

Whether investment in an ornament results in expression depends on the fighting quality and parental quality of the males, which so far has acted in isolation because we focussed on one of the two contexts. This situation changes when combining both models and male ornamentation can potentially acquire a function in both contexts simultaneously. A very important consideration is that 'quality' now becomes a two dimensional attribute and ornament expression is in various different ways correlated with the two underlying qualities. A second important component of the model is that the payoff of the Hawk-Dove conflict affects the reproductive success of brood, thus both male and female profit from these (potential) benefits. The reproductive success of a brood is therefore determined by a joint effect of the payoff from the Hawk-Dove game and parental qualities of the male. The sequence of events is as follows. At the start of a generation, each male will meet one opponent and may use his own fighting ability and the presence/absence of an ornament of the opponent to determine

which strategy to play in this Hawk-Dove game. Each female will then choose a partner from two candidates, and her choice may be affected by a preference. After the choice process, the pair will reproduce.

Model implementation

In order to accommodate all aspects as described, we need six variables for the full model:

i	frequency of ornament investment
p	frequency of preference for ornamented males
$h_{+,1}$	frequency of playing Hawk for a male with high fighting ability (+) confronted with an ornamented opponent (1).
$h_{+,0}$	frequency of playing Hawk for a male with high fighting ability (+) confronted with a non-ornamented opponent (0).
$h_{-,1}$	frequency of playing Hawk for a male with low fighting ability (–) confronted with an ornamented opponent (1).
$h_{-,0}$	frequency of playing Hawk for a male with low fighting ability (–) confronted with a non-ornamented opponent (0).

We assume that individuals are haploid and carry six gene loci, with free recombination between all loci. Each of the six loci corresponds to one of the six variables. At each locus, an allele can take the value 0 or 1. The allele on a given locus can change by mutation with a low probability μ. Generations are discrete and non-overlapping. The life-cycle of an individual is as follows: during reproduction the gametes of both parents fuse, after which recombination and meiosis takes place resulting in an individual with a haploid genotype. This individual is then assigned a fighting ability (+ or –) and a parental ability (+ or –), both with probability $\frac{1}{2}$. The individual may invest in an ornament (only males) but by doing so he pays a viability costs. The fighting and parental ability influences ornament expression, such that individuals with low abilities have reduced ornament expression. Similarly, a female may invest in expressing a preference, which also entails a viability cost. In the next step, all males engage in one contest which outcome will influence their reproductive success. In the last step, females will choose a male and reproduce.

With some additional assumptions it is possible in principle to translate the above described information into a population genetic model and derive recurrence equations describing the change of genotype frequencies over time. In practice this is a forbidding task since even for six diallelic loci the number of possible genotypes is very large ($2^6 = 64$). For this reason we make use of the quasi-linkage equilibrium technique (QLE; e.g. Kirkpatrick et al. 2002), which under the assumption of weak selection characterises the evolutionary dynamics by recurrence equation for the allele frequencies of the six loci:

Ornament investment: $\Delta i = \frac{1}{2} i(1-i)(\varepsilon\tilde{\sigma}_i + \varepsilon\tilde{\tau}_i)$ (1)

Preference: $\Delta p = \frac{1}{2} p(1-p)[\varepsilon^2(\tilde{\sigma}_p + \tilde{\omega}_p) + \varepsilon\tilde{\sigma}_{i,p}\Delta i]$ (2)

Strategy $h_{+,1}$: $\Delta h_{+,1} = \frac{1}{2} h_{+,1}(1-h_{+,1})\varepsilon\tilde{\sigma}_{h_{+,1}}$ (3)

Strategy $h_{+,0}$: $\Delta h_{+,0} = \frac{1}{2} h_{+,0}(1-h_{+,0})\varepsilon\tilde{\sigma}_{h_{+,0}}$ (4)

Strategy $h_{-,1}$: $\Delta h_{-,1} = \frac{1}{2} h_{-,1}(1-h_{-,1})\varepsilon\tilde{\sigma}_{h_{-,1}}$ (5)

Strategy $h_{-,0}$: $\Delta h_{-,0} = \frac{1}{2} h_{-,0}(1-h_{-,0})\varepsilon\tilde{\sigma}_{h_{-,0}}$ (6)

Notice that the allele frequency dynamics all have the same basic structure: the allele frequency change Δx is equal to $\frac{1}{2}$ (corresponding to sex limitation of the traits) times $x(1–x)$ (corresponding to the variance in allele frequencies) times the selection differential at the corresponding locus. The term ε quantifies the strength of selection. The QLE approximation (1) to (6) is valid for $\varepsilon \ll 1$. See appendix 7.1 for a detailed justification and the derivation of the selection differentials.

Male-male competition

The model assumptions

Depending on the allele at the investment locus, each male will decide on whether to invest in the ornament or not. Investing in the ornament comes at a cost c_i (an overview of all parameters and their meaning is given in table 7.1). Males with a high fighting ability who invest in the ornament will always express the ornament whereas males with a low fighting ability who invest in the ornament only express it with a probability η_f.

Table 7.1. Overview of the parameter used in the full model and a short description of their meaning.

symbol	description
V	value of resource in Hawk-Dove game
C	cost of losing escalated fight in Hawk-Dove game
b	direct benefits provided by the male
c_i	viability cost of investing in an ornament for males
c_p	viability cost of preference expression for females
α	fighting asymmetry: probability of winning an escalated fight is $\frac{1}{2}+\alpha$ for the high fighting ability male
γ	strength of female preference: probability to choose a preferred male is $\frac{1}{2}+\gamma$
η_f	probability for a male with low fighting quality that ornament investment leads to ornament expression
η_p	probability for a male with low parental quality that ornament investment leads to ornament expression

Each male is involved in one contest with a randomly assigned opponent. The choice of strategy played depends on one's own quality and ornament expression of the opponent. If both competitors play different strategies, the Hawk will get the resource of value V and the Dove will get 0. In case both play Dove, the resource is shared, and each male accrues a payoff of $\frac{1}{2}V$. The probability to win a Hawk-Hawk contest is determined by differences in fighting ability. If both competitors have the same fighting ability, each will have a probability of $\frac{1}{2}$ to win, but if they differ in fighting ability, the high-quality male will win with a probability $\frac{1}{2}+\alpha$ and the low quality male with probability $\frac{1}{2}-\alpha$. Hence, $\alpha(0 \leq \alpha \leq \frac{1}{2})$ is a measure for the asymmetry between high- and low-quality males. The payoff for the winner of the Hawk-Hawk conflict is V and for the loser C. In the special case of $\alpha=0$, the differences in 'fighting ability' do not have any physiological meaning and signalling evolving in this context is purely conventional (e.g. Maynard Smith and Parker 1976; Hurd 2006). The payoff acquired in the contest affects the individual's reproductive success and that of his breeding partner.

Signalling and non-signalling equilibria

It is conceivable that this system can attain different types of equilibria. To illustrate this, assume first that no individual invests in the ornament ($i=0$), hence no ornaments are being developed. This means that males can only base there strategic decisions on their own fighting capability and selection only acts on the strategy loci $h_{+,0}$ and $h_{-,0}$. A game theoretical analysis (see appendix 7.2) reveals that, depending on the relation between the fighting asymmetry α and the benefit-cost ratio V/C, three types of equilibria do exist which are illustrated in figure 7.2A. For $V/C<\frac{1}{2}$ the unique Nash equilibrium is given by $\hat{h}_{+,0} = 2V/C$ and $\hat{h}_{-,0} = 0$. From now on we refer to an equilibrium with $i=0$ as a 'non-signalling' equilibrium because the males base their decision on their own quality and no ornaments are expressed.

For a second extreme scenario imagine that all individuals invest in the ornament ($i = 1$). In this situation, all the four strategy loci will be affected by selection because there are both ornamented males (all high quality and a fraction η_f of the low quality individuals) and non-ornamented males (a fraction $1-\eta_f$ of the low quality individuals). Now it is no longer the case that the strategic behaviour at such 'signalling' equilibrium is uniquely determined by the model parameters. In fact, 'paradoxical' strategies (like individuals with low fighting ability playing Hawk when confronted with an ornamented opponent) may coexist with 'reasonable' strategies where high-quality individuals have a higher tendency to escalate then low-quality individuals. The unique Nash equilibrium with $\hat{h}_{-,1} = 0$ is illustrated in figure 7.2B. Notice that $\hat{h}_{+,1} = 1$ for all values of V/C while $\hat{h}_{-,0}$ and $\hat{h}_{+,1}$ are mixed strategies for small to moderate values of V/C. Furthermore notice that $\hat{h}_{-,0} \geq \hat{h}_{+,1}$

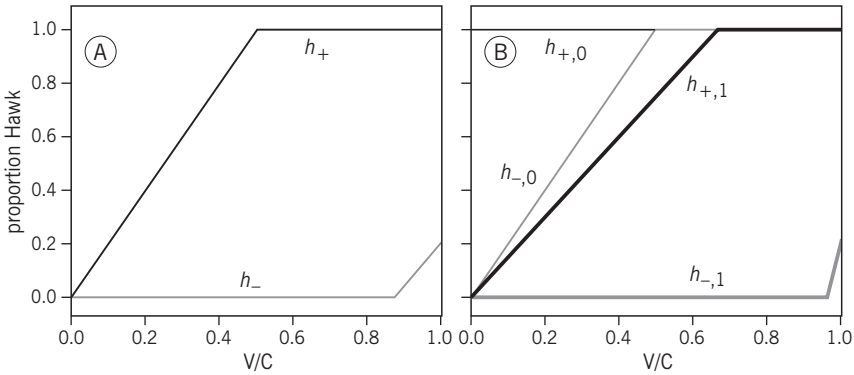

Figure 7.2. The equilibrium values for the situation where no male invests in an ornament ('non-signalling' equilibrium, A) and where all males invest in an ornament (signalling equilibrium, B). See appendix 7.2 for details.

Evolutionary dynamics

To explore the dynamics of the model we iterated system (1) to (6). As illustrated in figure 7.3, the full system can indeed evolve to either a signalling or a non-signalling equilibrium. If we start at $h_{+,1}=h_{+,0}=h_{-,1}=h_{-,0}= V/C$, the evolutionary stable strategy of the symmetric Hawk-Dove game, the system will typically end up at the non-signalling equilibrium (figure 7.3A). The system will only evolve to the signalling equilibrium if the vast majority of the initial population invests in the signal (i.e. i close to 1) (figure 7.3B). The parameter settings for these and other simulations presented in this paper can be found in table 7.2.

Table 7.2. Parameter values used in the figures.

parameter	figure					
	7.2	7.3	7.4	7.5	7.6	7.7–9
V	0.04	0.04	0.04	-	-	0.04
C	0.1	0.1	0.1	-	-	0.1
c_i	0.01	0.01	0.01	0.01	0.01	0.01
c_p	-	-	-	0.001	0.001	0.001
γ	-	-	-	0.05	0.05	0.05
α	0.25	variable	variable	-	-	0.25
b	-	-	-	variable	variable	0.05
η_f	0.5	0.4	variable	1	1	0.6
η_p	1	1	1	0.5	variable	0.4

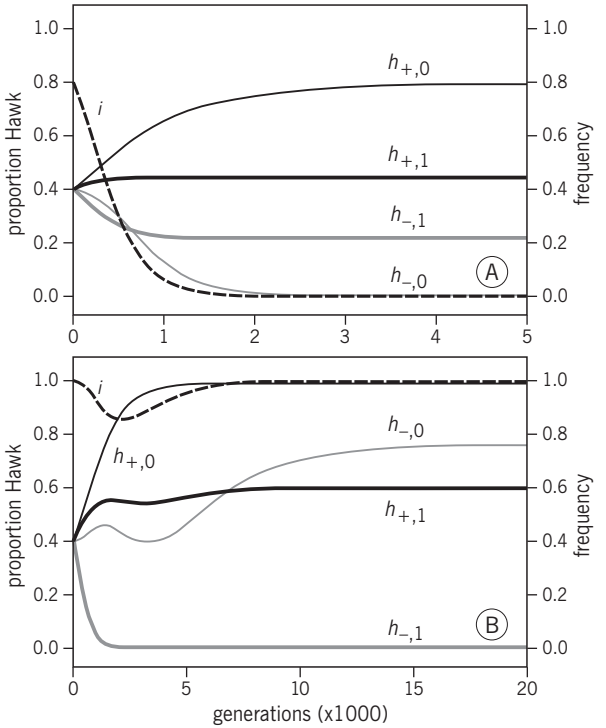

Figure 7.3. Two male-male competition simulation runs. The four strategy loci start at frequency *V/C*, the evolutionarily stable strategy of the symmetrical Hawk-Dove game. If the investment frequency is below a certain threshold value, the systems evolves to the non-signalling equilibrium (here the initial i is 0.8) (A). The threshold value for this particular model is very high; the system only evolves to the signalling equilibrium if i starts very close to 1 (B).

To get a more complete overview of the model behaviour we performed a bifurcation analysis with the program CONTENT (Kuznetsov and Levitin 1997). Figure 7.4 shows how the equilibrium pattern changes with a change in the parameter α (the asymmetry in fighting ability). It turns out that the non-signalling equilibrium is a stable equilibrium for each value of α ($0 < \alpha \leq \frac{1}{2}$; figure 7.4A). The signalling equilibrium is an alternative stable outcome (figure 7.4C) if α is below a certain threshold value (here $\alpha \leq \frac{1}{2} + \alpha \leq 0.88$). For values

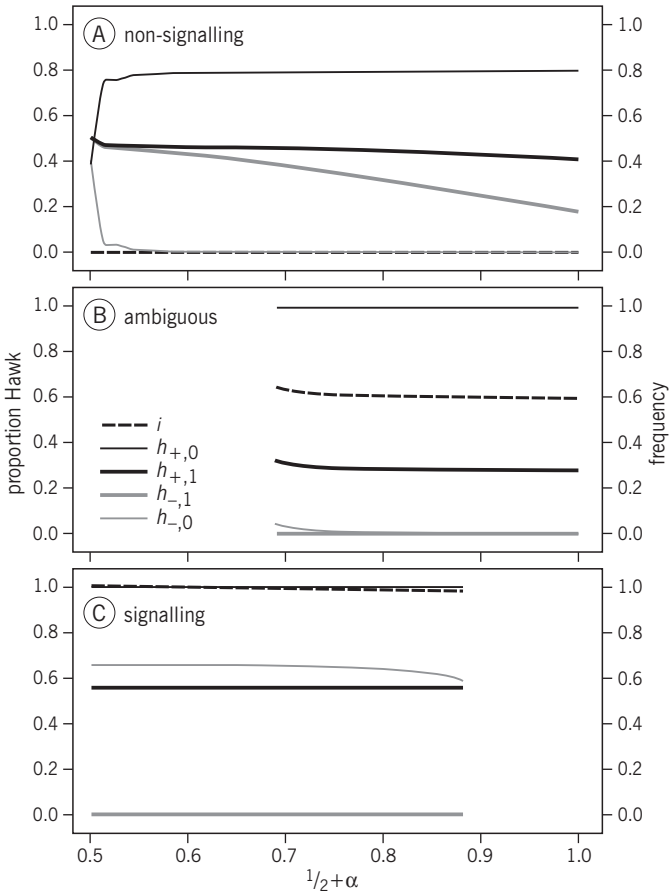

Figure 7.4. The three types of stable equilibria for male-male competition with the possibility of signal use. (A) For all values of the fighting asymmetry, α , the non-signalling equilibrium characterised by $i = 0$ is stable. (B) For large values of α , an 'ambiguous' investment strategy is an alternative stable equilibrium. Here, only a fraction of the population invests in the ornament and all low-quality males play Dove. (C) For small to moderate values of α a signalling equilibrium is an alternative stable outcome.

of α above a certain threshold value (here $\frac{1}{2}+\alpha \geq 0.69$) there exists a third, 'ambiguous' equilibrium in which only a fraction of the population invests in the ornament (figure 7.4B). At this equilibrium a pure Dove strategy is played by low-quality individuals (i.e. $\hat{h}_{-,0} = \hat{h}_{-,1} = 0$) while a pure Hawk strategy is played by high-quality individuals confronted with a non-ornamented opponent ($h_{+,0} = 1$). In none of the runs of our model a paradoxical signalling equilibrium was observed.

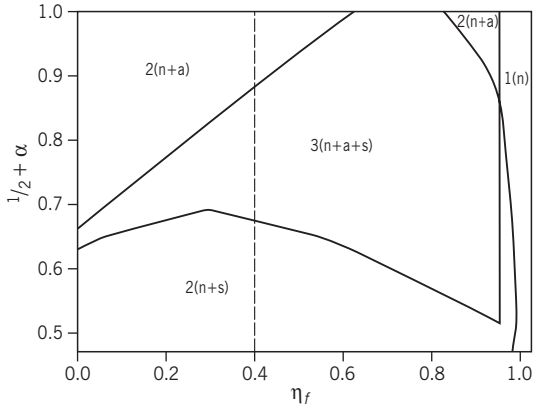

Figure 7.5. Bifurcation diagram showing the co-occurrence of the three types of equilibria depending on the model parameters α and η_f. The numbers refer to the number of coexisting equilibria while the types of equilibria are indicated in brackets (n = non-signalling, a = ambiguous and s = signalling). The dotted line indicates the η_f setting used in figure 7.4.

Female choice model

Model assumptions

Each female will mate once and has the choice between two randomly drawn males. Each female is either choosy or she mates at random. When a choosy female is confronted with two males differing in ornament expression, she mates with the ornamented male with a probability $\frac{1}{2}+\gamma$ and with the non-ornamented male with a probability $\frac{1}{2}-\gamma$. The variable p corresponds with the relative frequency of choosy females in the population. Expression of the preference is costly: females with a preference have to pay a viability cost c_p. Females benefit from mating with a male with high parental abilities, since in that case her reproductive success is increased by $b (b>0)$.

As before, males can invest in an ornament and the probability of this resulting in the expression of the ornament depends on the parental quality of the males. For simplicity we assume that investing males of high parental quality always express the ornament, while investing males of low parental quality will express the ornament with probability η_p.

Evolutionary dynamics

Direct benefit models of mate choice as considered here are relatively easy to understand (e.g. Kokko et al. 2003). For females it is beneficial to invest in a

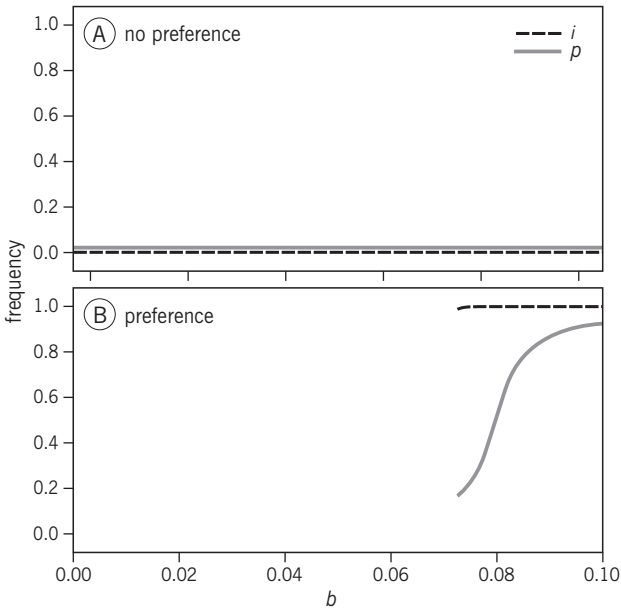

Figure 7.6. The two types of stable equilibria for female choice. (A) For all values of the direct benefits, b, the no preference equilibrium characterised by $p = 0$ is stable. (B) For large values of b, a second 'preference' equilibrium is an alternative stable equilibrium.

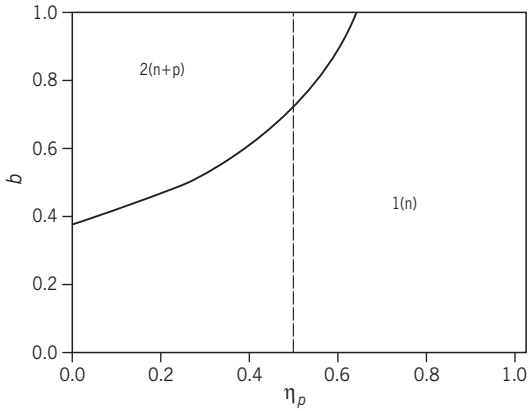

Figure 7.7. Bifurcation diagram showing the co-occurrence of the two types of equilibria for female choice depending on the model parameters b and η_p. The numbers refer to the number of coexisting equilibria while the types of equilibria are indicated in brackets (n = no preference and p = preference). The dotted line indicates the η_p setting used in figure 7.6.

preference for ornamented males if the costs of choice are outweighed by the benefits of this choice (i.e. a higher reproductive success due to mating with a male providing direct benefits). Iteration of the model shows that there are two types of equilibria which are illustrated in figure 7.6. For all values of b, $\hat{p} = 0$ (i.e. the absence of a preference) is a stable equilibrium. Obviously, the investment level of the males in the ornament is equal to zero when females do not exert preference for the ornament. If the direct benefits are larger than a threshold value, 'preference equilibrium' with $0 < \hat{p} \leq 1$ and $\hat{i} = 1$ is an alternative stable strategy.

Dual-function signalling

Dual quality and ornament expression

After these preparations, we are now able to link signalling in the contexts of male-male competition and female choice in an integrative model. In comparison to the constituent models, we now have to face the difficulty that male quality is a two-dimensional trait, consisting of fighting ability and parental ability. It is therefore no longer straightforward to translate a male's investment into the ornament into quality-dependent expression of the ornament. We chose to implement this in a multiplicative way, corresponding to the assumption that both quality components affect ornament expression in the same way, and that there are no synergistic effects between the quality components. To be more explicit, we assumed that the probability that an investing male actually expresses the ornament is given by:

1 , if male has high fighting and high parental ability;
η_p , if male has high fighting and low parental ability;
η_f , if male has low fighting and high parental ability;
$\eta_p \eta_f$, if male has low fighting and low parental ability.

Notice that the joint effect of both quality components on ornament expression has important implications on both male-male competition and female choice, since the ornament becomes a less reliable indicator of each of the constituent quality components. For example, an investing male with high fighting ability does no longer automatically express the ornament (if it has low parental ability). As a consequence, in a population with maximal investment (i.e. $\hat{i} = 1$), the fact that one's opponent does not have an ornament does not imply that the opponent has low fighting ability. In other words, in the combined model the information content of the signal is inherently lower than in the constituent models, and this in turn should impede the evolution of costly signalling.

Analysis of the integrated model

We can now investigate whether, and under what conditions, signals with a dual function can evolve. In particular, we are interested in the question whether female choice affects signalling in male-male competition, and vice versa. Moreover, we will address how the strategic behaviour in the Hawk-Dove game (i.e. the strategies $\hat{h}_{+,1}$, $\hat{h}_{+,0}$, $\hat{h}_{-,1}$, $\hat{h}_{-,0}$,) and/or the frequency of female preference ($\hat{p}$) is affected when a signal gets an additional function.

To study these questions, we first perform an equilibrium analysis in the combined model for each of the contexts (i.e. male-male competition or female choice) in isolation. This is necessary because in the combined model signals are inherently less reliable than in each constituent model. Starting from a male-male competition (respectively female choice) equilibrium, we then add the possibility for signalling to evolve in the complementary context.

We choose the following parameter combination: $V = 0.04$, $C = 0.1$, $c_i = 0.01$, $c_p = 0.001$, $\gamma = 0.05$, $\alpha = 0.2$, $b = 0.05$, $\eta_f = 0.6$ and $\eta_p = 0.4$. In line with figure 7.6, a female preference would not evolve as a single function for these parameters. Based on figure 7.4, one might expect three types of equilibria in the male-male competition context. However, it turns out that the signalling equilibrium ceases to exist in the combined model, because now the signal is less informative than in the constituent model on which figure 7.4 is based. In other words, only the non-signalling equilibrium and the ambiguous equilibrium are feasible as single-function equilibria in the male-male context.

Evolution of a dual-function signal

Let us start with the ambiguous signalling equilibrium in the male-male context. Figure 7.8 shows that allowing female preferences to evolve does indeed have important implications. First, the females express a preference for the same parameters for which this was not feasible in the single-function context. Second, the ambiguous male-male signalling equilibrium is turned into a 'full-fledged' signalling equilibrium where all the males invest into the signal. This example clearly demonstrates that dual-function signals can evolve, and that signalling in one context can facilitate the evolution of signalling in the other context.

Getting signalling off the ground

In the previous example, we started with a situation where already some males invested into the developing an ornament. It is less straightforward to study the effect of female choice on the non-signalling equilibrium in male-male interaction, and the effect of male-male competition on the no preference equilibrium in female choice. In fact, we know already that non-signalling, respectively no preference, is a stable equilibrium in the constituent models for all parameter combinations. This remains to be the case in the combined model: preference

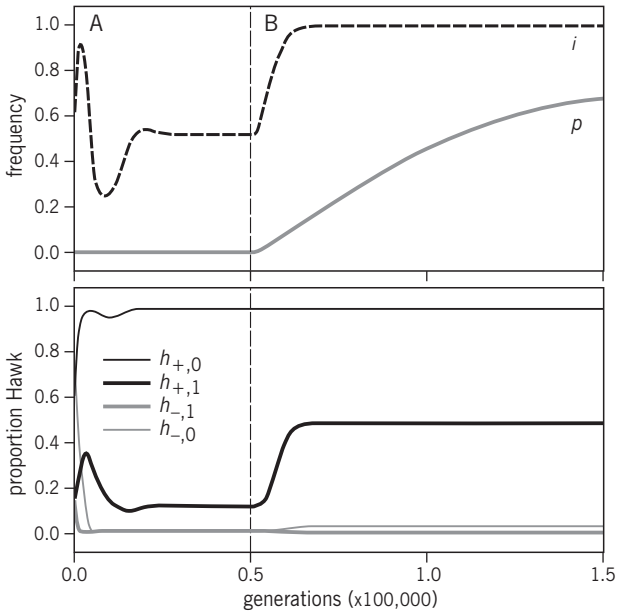

Figure 7.8. In the first part of the figure (A), male-male competition evolves towards the ambiguous signalling equilibrium. At a certain moment (indicated by the dashed lines) the female preference is introduced and a preference evolves (B). The ornament investment and preference frequencies are depicted in the upper panel, the allele frequencies of the four strategy loci in the lower panel.

cannot spread in the non-signalling equilibrium and signalling cannot spread in the non-preference equilibrium.

Still, we can study the question whether the stability of the no preference/non-signalling equilibrium is affected by allowing the signal to attain a dual function. To this end, we perform a perturbation analysis that will provide us with insights in whether signalling can get 'off the ground' more easily if the signal has a dual function.

Evolution of male-male signalling through female preference

We tested the stability of the non-signalling male-male equilibrium in the absence of female choice by repeatedly perturbing this equilibrium by introducing a higher frequency of investing males. In each case, the population rapidly returned to its initial state. This is in line with figure 7.2, which illustrates that in the male-male competition model alone, it is extremely difficult to get signalling off the ground. The situation changes if female preferences can

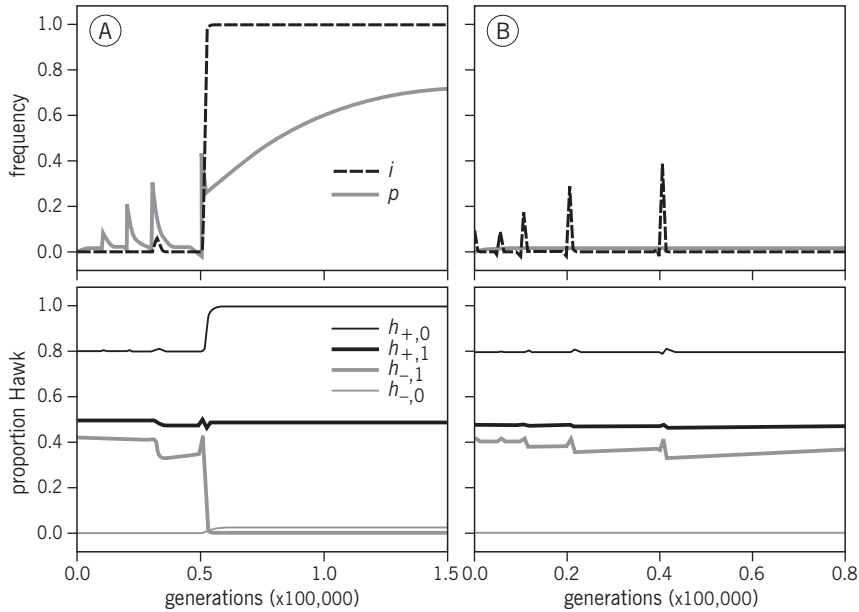

Figure 7.9. In both panel A and B male-male competition starts at the non-signalling equilibrium and female choice at the no preference equilibrium. In A, the initial frequencies of the preference in the population are perturbed to test if signalling can evolve. In B, the initial frequency of ornament investment is similarly perturbed.
The ornament investment and preference frequencies are depicted in the upper panel, the allele frequencies of the four strategy loci in the lower panel.

evolve as well. In part A of the figure 7.9 it becomes clear that, when the perturbation of the female preference is large enough, all males invest in the ornament, the non-signalling equilibrium shifts to the signalling equilibrium and the female preference equilibrium is attained.

Evolution of female preference through male-male signalling

For the parameters chosen, female preference cannot evolve if the signal only functions in a female choice context. This was tested by perturbing the by introducing a large frequency of females expressing a preference. Similarly to the male-male equilibrium, all frequencies returned to the initial conditions. This situation did not change when signal use in male-male competition was set free to evolve. Perturbations of the initial frequencies of investing males did not change the female preference equilibrium, nor the non-signalling equilibrium in male-male competition (figure 7.9B).

Conclusions and Implication

In this paper we provide proof of principle that dual-function signalling can evolve. Importantly, we find that male-male competition and female choice synergistically affect the evolution of signalling, i.e. signalling equilibria are more easily attained when the signal can have a dual function. A dual function of a signal affects the equilibria reached in comparison to a single function context. We find that ornament investment by males increases with a dual function and the strategic choices made in male-male competition change accordingly. Similarly, the female preference increases in the population. However, our results also emphasize the difficulties of destabilising the non-signalling equilibrium; in other words, the use of signals in either context is not trivial. Although our results show that the possibility of signal use in multiple contexts might facilitate the commencement of signal use, it remains to be quantified how significant this effect is.

We are aware that with this analysis, we have not more than scratched the surface of signal use in more multiple contexts. The kind of models as used in this study is notoriously intricate and not easy to analyse. For this reason we have, for this first attempt, made a large number of simplifying assumptions:

- the quality components interact multiplicatively, which assumes that both components have a similar effect on ornament expression and don't, for example, work synergistically.
- only direct benefits are considered. This excludes models based on heritable quality components such as 'good genes' models which are widely used in sexual selection theory.
- females can profit twice; from direct benefits obtained by males in the contest and parental quality of the male. An obvious alternative is that contests between males only influence their mating chance.
- the ornament can only be present or absent; it cannot take on an intermediate value which would be required if the ornament would be a revealing handicap.
- males cannot base their investment strategies on their own quality. Such condition dependent investment can create complex non-equilibrium dynamics (van Doorn and Weissing 2006) and was therefore excluded.
- male contest strategy can only depend on own quality, but not on own ornament expression.

Even with these simplifications, the analysis of the resulting models is difficult. Here we made use of the QLE technique, which is only applicable in cases of weak selection, but which has the huge advantage that the dimensionality of the problem is reduced enormously (from 2^6 to 6 recurrence equations). Individual based simulations can be used to test how robust our results are against

violations of the weak selection assumption. Furthermore, these models allow us to explore the effects of stochastic processes, such as drift, on the dynamics of the systems. Parts of our model have been analysed using individual based simulations and this validated the results obtained by the QLE technique.

The model presented here should be seen as a first step trying to link signalling processes in different sexual selection contexts. If successful, this might lead towards a more unifying theory of sexual selection.

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Appendix 7.1

The Evolution of Dual-Function Signals

Appendix - derivation of population-genetic equations

1 - Introduction

This appendix outlines the derivation of the population-genetic recurrence equations presented in the main text. Rather than deriving equations for genotype frequencies, as one would normally do, we derive equations for the change of *genetical associations* (i.e., statistical moments of the genotype frequency distribution) from one generation to the next. For an explanation of this technique we refer to

M. Kirkpatrick, T. Johnson and N. Barton (2002), General Models of Multilocus Evolution, *Genetics* 161: 1727-1750.

This appendix consists of four parts. After this introductory part, we define *Mathematica* procedures to calculate how selection and sexual reproduction affect the genetical associations (part 2 - the toolbox). Next, we calculate the selection coefficients that act on individual allele frequencies or on genetical associations between sets of alleles (part 3 - selection coefficients). In the final part of this appendix, we derive approximations for the change of allele frequencies from one generation to the next.
This appendix was written in *Mathematica* (Wolfram, 2003), and is provided in two versions. This printed version is a summary of a complete *Mathematica* worksheet that is available from the authors on request or at
http://www.rug.nl/biologie/onderzoek/onderzoeksgroepen/theoreticalbiology/index. The complete version can be used to verify the calculations.

2 - The Toolbox

▪ Preliminaries - definition of positions and reference values

The evolving characters of our model are encoded by six loci, one locus for each character. Each locus segregates for two alleles. We keep track of the allele frequencies (denoted f_k for locus k) and of the statistical associations between allele frequencies at different loci (denoted by $\mathfrak{D}[\mathbb{A}]$, where $\mathbb{A}$ may represent any set of loci).

In the procedures defined below, we use $\mathbb{P} = \{p\}$, $\mathbb{I} = \{i\}$ and $\mathbb{H} = \{h1, h2, h3, h4\}$ to denote the sets of loci influencing female mating preference, male ornament investment and the male's

strategy in the Hawk-Dove game,respectively. Furthermore, we define $\mathbb{M} = \mathbb{I} \bigcup \mathbb{H}$ and $\mathbb{W} = \mathbb{M} \bigcup \mathbb{P}$.

Genetical associations are defined with respect to a set of reference values that can be arbitrarily chosen. We choose the reference values equal to the allele frequencies at the zygote stage since this causes first-order associations at the zygote stage to vanish.

■ Procedures

In the following section we implement five procedures that are used to derive our model equations. The first one is needed to expand associations with repeated indices.

```
removeDupl[Asctn_, A_List, B_List] :=
 Module[{AB, dupl, k},
  AB = Join[A, B];
  If[Length[AB] > 0,
   If[dupl = Do[
      If[Count[AB, AB[[k]]] > 1, Return[AB[[k]]],]
      , {k, 1, Length[AB]}
     ]; MemberQ[AB, dupl],
    Return[℘dupl (1 - ℘dupl) removeDupl[Asctn, DeleteCases[
        A, dupl], DeleteCases[B, dupl]] + (1 - 2 ℘dupl)
      removeDupl[Asctn, A, DeleteCases[B, dupl]]],
    Return[Asctn[Sort[Join[A, B]]]]],
   Return[Asctn[{}]]]
 ]
```

Viability selection changes the genetical associations. We use the following procedure to express genetical associations in female and male adults (denoted by $\mathcal{D}_f[\mathbb{A}]$ and $\mathcal{D}_m[\mathbb{A}]$, respectively) in terms of genetical associations in zygotes (denoted as $\mathcal{D}_0[\mathbb{A}]$).

```
selection = {𝒟f[A_List] :>
    Module[{C, dsum = 𝒟0[A] , k},
     C = Subsets[ℙ];
     Do[
      dsum += ωC[[k]] (removeDupl[𝒟0, A, C[[k]]] -
          𝒟0[A] 𝒟0[C[[k]]]), {k, 1, Length[C]}];
     dsum /. referencevalues
    ],
   𝒟m[A_List] :>
    Module[{C, dsum = 𝒟0[A], k},
     C = Subsets[𝕀];
     Do[
      dsum += τC[[k]] (removeDupl[𝒟0, A, C[[k]]] -
          𝒟0[A] 𝒟0[C[[k]]]), {k, 1, Length[C]}];
     dsum
    ]
  };
```

The coefficients $\tau_{\mathbb{A}}$ and $\omega_{\mathbb{A}}$ represent selection coefficients that capture the effect of selection on the loci in the set $\mathbb{A}$. The values of these selection coefficients will be calculated in part 3 below.

The surviving adults form mating groups and reproduce sexually. The process of sexual selection, i.e., the conflict between the males and the subsequent choice of a mate by the female, is modelled by a single step of selection at the level of the mating group. A mating group is defined by the genotype of the female (loci with subscript *f*) and the genotypes of the two males (loci with subscripts m_1 and m_2) between whom she chooses. The fitness of a mating group reflects the probability that the female chooses to mate with the first male. The next procedure is used to map the genetical associations in the eventual mating pair back to associations in males and females after viability selection.

```
reproduction = 𝒟p[A_List] :>
   Module[{Af, Am1, S, dsum , k, Uf, Um1, Um2},
    Af =
     Complement[A, Replace[𝕎, x_ → xm , 1]] /. {x_f → x};
    Am1 = Complement[A, Replace[𝕎, x_ → xf , 1]] /.
      {x_m → x};
    S = Subsets[Join[Replace[ℙ, x_ → xf , 1], Replace[
        𝕄, x_ → xm1 , 1], Replace[𝕄, x_ → xm2 , 1]], 2];
    dsum =  𝒟f [Af] 𝒟m [Am1];
    Do[
     Uf = DeleteCases[S[[k]], _m_ ] /. {x_f → x};
     Um1 = DeleteCases[
        DeleteCases[S[[k]], _m2 ], _f ] /. {x_m1 → x};
     Um2 = DeleteCases[DeleteCases[S[[k]], _m1 ], _f ] /.
       {x_m2 → x};
     dsum += σSort[S[[k]]] (removeDupl[𝒟f , Af, Uf]
          removeDupl[𝒟m , Am1, Um1] 𝒟m [Um2] -
         𝒟f [Af] 𝒟m [Am1] 𝒟f [Uf] 𝒟m [Um1] 𝒟m [Um2]),
     {k, 1, Length[S]}];
    dsum /. {𝒟f [{}] → 1, 𝒟m [{}] → 1}
   ];
```

After mating pairs are formed, the female and male in the pair produce offspring. To calculate the values of association in the offspring, we use the following procedure. For simplicity, we assume free recombination between loci.

```
transmission = 𝒟z [A_List] :>
   Module[
    {B = Subsets[A], Af, Am, k, tc = 1 / 2^Length[A] , dsum = 0},
    Do[
     Af = Replace[B[[k]], x_ → xf , 1];
     Am = Replace[Complement[A, B[[k]]], x_ → xm , 1];
     dsum += tc 𝒟p [Sort[Join[Af, Am]]], {k, 1, Length[B]}];
    dsum /. 𝒟p [{}] → 1
   ];
```

The value of any given association can now be expressed in terms of associations at earlier phases of the lifecycle. In particular, by applying the following substitution rule, which traces its way back through a complete lifecycle, we can calculate how an association changes from one generation to the next.

```
lifeCycle =
  eq_ :→ (eq /. changeReferenceValues /. transmission /.
       reproduction /. selection /. referencevalues);
```

From here on, we assume that selection is weak. For example, we assume that $\tau_{[i]}$ can be written as $\epsilon \tilde{\tau}_{[i]}$ where $\epsilon \ll 1$ and $\tilde{\tau}_{[i]} = \mathcal{O}[1]$. An analogous situation applies to all other selection coefficients. As is common in sexual selection models we assume moreover that direct selection on female preference is weak relative to other selection pressures. Hence, $\omega_{[p]} = \mathcal{O}[\epsilon^2]$. Since selection is weak relative to recombination, the genetical associations between loci will tend to be small. This allows us, later on, to drastically simplify the model by means of a Quasi-Linkage-Equilibrium (QLE) approximation.

3 - Selection coefficients

So far we have treated the selection coefficients as unspecified coefficients $\sigma_{\mathbb{A}}$, $\tau_{\mathbb{A}}$ and $\omega_{\mathbb{A}}$. In this section we calculate the actual values of these coefficients. To do that, we need to define procedures to express the fitness of a genotype as a sum of contributions from individual loci and associations between loci, as detailed in Kirkpatrick, Johnson & Barton (2002). We will first calculate the viability selection coefficients, and then proceed to calculate the more intricate sexual selection coefficients.

Only a single locus is exposed directly to viability selection in males. The following procedure expresses the fitness of the two possible genotypes at this single locus in terms of allele frequencies and the selection coefficient $\tau_{[i]}$.

```
eqTau[G_List] :=
 Module[{A = Subsets[𝕀], B, sms = 1, j, k, ζ},
  Do[
   ζ = 1;
   B = A[[k]];
   Do[ζ *=
     (G[[First[Flatten[Position[𝕀, B[[j]]]]]]] - ℘B[[j]]),
    {j, 1, Length[B]}];
   sms += τA[[k]] (ζ - 𝒟0[A[[k]]]), {k, 1, Length[A]}];
  sms /. referencevalues /. qle]
```

To calculate the value of the selection coefficient $\tilde{\tau}_{[i]}$, we equate the above to expression to their corresponding fitness values, and solve the resulting system of equations. Ignoring terms of order ϵ and above, we find

```
tauSubs = Solve[
    {
     eqTau[{0}] == 1/w̄ᵢ,
     eqTau[{1}] == (1 - ϵ cᵢ)/w̄ᵢ
    }, {τ̃{i}, w̄ᵢ}] /. {ϵ → 0} // Flatten
```

$$\{\tilde{\tau}_{\{i\}} \to -c_i,\ \bar{w}_i \to 1\}$$

where $\bar{w}_i$represents the mean viability of males.

An analogous procedure is used to solve for the selection coefficients that are involved in female viability selection.

```
omegaSubs = Solve[
    {
     eqOmega[{0}] == 1/w̄ₚ,
     eqOmega[{1}] == (1 - ϵ² cₚ)/w̄ₚ
    }, {ω̃{p}, w̄ₚ}] /. {ϵ → 0} // Flatten
```

$$\{\tilde{\omega}_{\{p\}} \to -c_p,\ \bar{w}_p \to 1\}$$

The procedure for calculating the sexual selection coefficients $\sigma_{\mathbb{A}}$ is slightly more complicated, but is based on the same principle. First, we define a procedure to decompose fitness into contributions attributable to individual alleles and associations of alleles.

```
eqSigma[Gf_List, Gm1_List, Gm2_List, order_] :=
 Module[{S, j, k, Uf, Um1, Um2, sms = 1, ℘},
  S = Subsets[Join[Replace[ℙ, x_ → x_f, 1],
     Replace[𝕄, x_ → x_m1, 1], Replace[𝕄, x_ → x_m2, 1]], 2];
  Do[
   Uf = DeleteCases[S[[k]], _m_] /. {x__f → x};
   Um1 = DeleteCases[
      DeleteCases[S[[k]], _m2], _f] /. {x__m1 → x};
   Um2 = DeleteCases[DeleteCases[S[[k]], _m1], _f] /.
     {x__m2 → x};
   ℘ = 1;
   Do[℘ *=
     (Gf[[First[Flatten[Position[ℙ, Uf[[j]]]]]]] - ℘Uf[[j]]),
    {j, 1, Length[Uf]}];
```

```
    Do[ξ *= (Gm1[[First[Flatten[Position[M, Um1[[j]]]]]]] -
        ϖ_Um1[[j]]), {j, 1, Length[Um1]}];
    Do[ξ *= (Gm2[[First[Flatten[Position[M, Um2[[j]]]]]]] -
        ϖ_Um2[[j]]), {j, 1, Length[Um2]}];
    sms += σ_Sort[S[[k]]] (ξ - D_f[Uf] D_m[Um1] D_m[Um2]),
    {k, 1, Length[S]}];
   Series[sms /. selection /. referencevalues /. qle,
     {ϵ, 0, order}] // Normal ]
```

To calculate the fitness of this mating group, we define a procedure 'fitness', which implements the details of our biological model.

```
fitness[Gf_List, Gm1_List, Gm2_List, order_] :=
 Module[{qp1, qp2, qf1, qf2, probt1, probt2, t1,
   t2, h1, h2, pwinfight, plosefight, pwin, plose,
   pequal, offspring, pt1, pt2, ftns, cpf1, cpf2},
  probt1 = Gm1[[5]] η0 η_f^(1-qf1) η_p^(1-qp1);
  probt2 = Gm2[[5]] η0 η_f^(1-qf2) η_p^(1-qp2);
  h1 = Gm1[[1]] qf1 t2 + Gm1[[2]] qf1 (1 - t2) +
    Gm1[[3]] (1 - qf1) t2 + Gm1[[4]] (1 - qf1) (1 - t2);
  h2 = Gm2[[1]] qf2 t1 + Gm2[[2]] qf2 (1 - t1) +
    Gm2[[3]] (1 - qf2) t1 + Gm2[[4]] (1 - qf2) (1 - t1);
  pwin = h1 (1 - h2);
  plose = (1 - h1) h2;
  pwinfight = h1 h2 (1 / 2 (qf1 qf2 + (1 - qf1) (1 - qf2)) +
      α (1 - qf2) qf1 + (1 - α) (1 - qf1) qf2);
  plosefight = h1 h2 (1 / 2 (qf1 qf2 + (1 - qf1) (1 - qf2)) +
      α (1 - qf1) qf2 + (1 - α) (1 - qf2) qf1);
  pequal = (1 - h1) (1 - h2);
                                1 + ϵ γ Gf[[1]] t1
  offspring = ------------------------------------
              2 + ϵ γ Gf[[1]] t1 + ϵ γ Gf[[1]] t2
    (pequal (1 + ϵ V / 2) + (pwin + pwinfight) (1 + ϵ V) +
      (plose + plosefight (1 - ϵ C)));

  pt1 = 1 - t1 - (1 - 2 t1) probt1;
  pt2 = 1 - t2 - (1 - 2 t2) probt2;
  cpf1 =
   qp1 qf1 + (1 - qp1) (1 - qf1) - qp1 (1 - qf1) - qf1 (1 - qp1);
  cpf2 = qp2 qf2 + (1 - qp2) (1 - qf2) -
    qp2 (1 - qf2) - qf2 (1 - qp2);
  Series[Sum[pt1 (1 + ρ cpf1) pt2 (1 + ρ cpf2) offspring
       (1 + ϵ b (qp1 - 1 / 2)), {qp1, 0, 1}, {qp2, 0, 1},
      {qf1, 0, 1}, {qf2, 0, 1}, {t1, 0, 1}, {t2, 0, 1}] /
     (8 (1 + ϵ w̃)), {ϵ, 0, order}] // Normal
 ]
```

▪ Equations for the sexual selection coefficients

By averaging over different combinations of genotypes, we obtain equations for each of the sexual selection coefficients that are needed for our analysis.

For example, this is the equation that determines the value of $\tilde{\sigma}_{\{h1_{m1}\}}$:

```
eq3 = averagingProc[{{0, 1}},
  {{0}, {0, 1}, {0, 1}, {0, 1}, {0, 1}},
  {{0, 1}, {0, 1}, {0, 1}, {0, 1}, {0, 1}}, 1]
```

$$-\frac{1}{32}\,\epsilon\,(-1+f_{h1})\,f_{h1}\,(f_i^2\,\eta_0^2\,(-1-\rho+(-1+\rho)\,\eta_p)\,(C\,f_{h1}\,(-1-\rho+(-1+\rho)\,\eta_p)+C\,f_{h2}\,(1+\rho+\eta_p-\rho\,\eta_p)+(-2\,C-V+2\,(C+V)\,\alpha)\,(f_{h3}-f_{h4})\,\eta_f\,(1-\rho+(1+\rho)\,\eta_p))-2\,f_i\,\eta_0\,(C\,f_{h2}\,(-1-\rho+(-1+\rho)\,\eta_p)+V\,(1+\rho+\eta_p-\rho\,\eta_p)+(V+(-2\,C-V+2\,(C+V)\,\alpha)\,f_{h4})\,\eta_f\,(1-\rho+(1+\rho)\,\eta_p))+32\,\tilde{\sigma}_{\{h1_{m_1}\}})$$

Thirteen different selection coefficients appear in the QLE approximation of or model (see the next section). In order to solve for these coefficients, we derive fourteen equations like the one above. We solve separately for the first and second order components of the selection coefficient acting on the female preference allele (see the online version of this worksheet) and then solve for the remaining selection coefficients.

```
selCoeff =
 Solve[{eq1 == 0, eq2 == 0, eq3 == 0, eq4 == 0, eq5 == 0, eq6 == 0,
     eq7 == 0, eq8 == 0, eq9 == 0, eq10 == 0, eq11 == 0, eq12 == 0,
     eq13 == 0, eq14 == 0}, {σ̃{pf}, σ̃{i_m1}, σ̃{h1_m1}, σ̃{h2_m1},
     σ̃{h3_m1}, σ̃{h4_m1}, σ̃{i_m2}, σ̃{h1_m1,pf}, σ̃{h2_m1,pf}, σ̃{h3_m1,pf},
     σ̃{h4_m1,pf}, σ̃{i_m1,pf}, σ̃{i_m2,pf}}] // Flatten // FullSimplify
```

$$\{\tilde{\sigma}_{\{h1_{m_1},p_f\}}\to 0,\ \tilde{\sigma}_{\{h2_{m_1},p_f\}}\to 0,\ \tilde{\sigma}_{\{h3_{m_1},p_f\}}\to 0,\ \tilde{\sigma}_{\{h4_{m_1},p_f\}}\to 0,$$

$$\tilde{\sigma}_{\{i_{m_1},p_f\}}\to\frac{1}{8}\,\gamma\,\eta_0\,(1+\rho-(-1+\rho)\,\eta_p+\eta_f\,(1-\rho+(1+\rho)\,\eta_p)),$$

$$\tilde{\sigma}_{\{i_{m_2},p_f\}}\to-\frac{1}{8}\,\gamma\,\eta_0\,(1+\rho-(-1+\rho)\,\eta_p+\eta_f\,(1-\rho+(1+\rho)\,\eta_p)),$$

$$\tilde{\sigma}_{\{i_{m_1}\}}\to-\frac{1}{32}\,\eta_0\,(2\,V\,f_{h3}+2\,V\,\rho\,f_{h3}-2\,V\,f_{h4}-2\,V\,\rho\,f_{h4}-4\,\gamma\,f_p-4\,\gamma\,\rho\,f_p+2\,V\,f_{h3}\,\eta_f-2\,V\,\rho\,f_{h3}\,\eta_f-2\,V\,f_{h4}\,\eta_f+2\,V\,\rho\,f_{h4}\,\eta_f+2\,C\,f_{h3}\,f_{h4}\,\eta_f-2\,C\,\rho\,f_{h3}\,f_{h4}\,\eta_f-2\,C\,f_{h4}^2\,\eta_f+2\,C\,\rho\,f_{h4}^2\,\eta_f-4\,\gamma\,f_p\,\eta_f+4\,\gamma\,\rho\,f_p\,\eta_f+C\,f_{h3}^2\,f_i\,\eta_0\,\eta_f^2-2\,C\,\rho\,f_{h3}^2\,f_i\,\eta_0\,\eta_f^2+C\,\rho^2\,f_{h3}^2\,f_i\,\eta_0\,\eta_f^2-2\,C\,f_{h3}\,f_{h4}\,f_i\,\eta_0\,\eta_f^2+4\,C\,\rho\,f_{h3}\,f_{h4}\,f_i\,\eta_0\,\eta_f^2-2\,C\,\rho^2\,f_{h3}\,f_{h4}\,f_i\,\eta_0\,\eta_f^2+C\,f_{h4}^2\,f_i\,\eta_0\,\eta_f^2-2\,C\,\rho\,f_{h4}^2\,f_i\,\eta_0\,\eta_f^2+C\,\rho^2\,f_{h4}^2\,f_i\,\eta_0\,\eta_f^2+2\,(-(-1+\rho)\,(V\,f_{h3}-V\,f_{h4}-2\,\gamma\,f_p)+(1+\rho)\,((f_{h3}-f_{h4})\,(V+C\,f_{h4})-2\,\gamma\,f_p)\,\eta_f-C\,(-1+\rho^2)\,(f_{h3}-f_{h4})^2\,f_i\,\eta_0\,\eta_f^2)\,\eta_p+C\,(1+\rho)^2\,(f_{h3}-f_{h4})^2\,f_i\,\eta_0\,\eta_f^2\,\eta_p^2+C\,f_{h1}^2\,f_i\,\eta_0\,(1+\rho-(-1+\rho)\,\eta_p)^2+C\,f_{h2}^2\,(-1-\rho+(-1+\rho)\,\eta_p)\,(2+f_i\,\eta_0\,(-1-\rho+(-1+\rho)\,\eta_p))+2\,f_{h1}\,(V\,(1+\rho-(-1+\rho)\,\eta_p)-C\,f_{h2}\,(-1-\rho+(-1+\rho)\,\eta_p)\,(1+f_i\,\eta_0\,(-1-\rho+(-1+\rho)\,\eta_p))+$$

$$\eta_f\ (1-\rho+(1+\rho)\ \eta_p)\ (V+C\ f_{h3}\ f_i\ \eta_0\ (1+\rho+\eta_p-\rho\ \eta_p)+$$
$$f_{h4}\ (-V+2\ (C+V)\ \alpha+C\ f_i\ \eta_0\ (-1-\rho+(-1+\rho)\ \eta_p))))+$$
$$2\ f_{h2}\ (-V\ (1+\rho+\eta_p-\rho\ \eta_p+\eta_f\ (1-\rho+(1+\rho)\ \eta_p))+$$
$$f_{h3}\ (-1-\rho+(-1+\rho)\ \eta_p)$$
$$(-2\ C-V+2\ (C+V)\ \alpha+C\ f_i\ \eta_0\ \eta_f\ (1-\rho+(1+\rho)\ \eta_p))+$$
$$f_{h4}\ (-(-2\ C-V+2\ (C+V)\ \alpha)\ (-1-\rho+(-1+\rho)\ \eta_p)-$$
$$\eta_f\ (1-\rho+(1+\rho)\ \eta_p)$$
$$(-V+2\ (C+V)\ \alpha+C\ f_i\ \eta_0\ (-1-\rho+(-1+\rho)\ \eta_p)))))),$$

$$\sigma_{\{h1_{m_1}\}} \to \frac{1}{32}\ f_i\ \eta_0\ (-2\ V\ \rho\ \eta_f-4\ C\ f_{h4}\ \eta_f-2\ V\ f_{h4}\ \eta_f+$$
$$4\ C\ \alpha\ f_{h4}\ \eta_f+4\ V\ \alpha\ f_{h4}\ \eta_f+4\ C\ \rho\ f_{h4}\ \eta_f+2\ V\ \rho\ f_{h4}\ \eta_f-$$
$$4\ C\ \alpha\ \rho\ f_{h4}\ \eta_f-4\ V\ \alpha\ \rho\ f_{h4}\ \eta_f-2\ C\ f_{h3}\ f_i\ \eta_0\ \eta_f-$$
$$V\ f_{h3}\ f_i\ \eta_0\ \eta_f+2\ C\ \alpha\ f_{h3}\ f_i\ \eta_0\ \eta_f+2\ V\ \alpha\ f_{h3}\ f_i\ \eta_0\ \eta_f+$$
$$2\ C\ \rho^2\ f_{h3}\ f_i\ \eta_0\ \eta_f+V\ \rho^2\ f_{h3}\ f_i\ \eta_0\ \eta_f-$$
$$2\ C\ \alpha\ \rho^2\ f_{h3}\ f_i\ \eta_0\ \eta_f-2\ V\ \alpha\ \rho^2\ f_{h3}\ f_i\ \eta_0\ \eta_f+$$
$$2\ C\ f_{h4}\ f_i\ \eta_0\ \eta_f+V\ f_{h4}\ f_i\ \eta_0\ \eta_f-2\ C\ \alpha\ f_{h4}\ f_i\ \eta_0\ \eta_f-$$
$$2\ V\ \alpha\ f_{h4}\ f_i\ \eta_0\ \eta_f-2\ C\ \rho^2\ f_{h4}\ f_i\ \eta_0\ \eta_f-$$
$$V\ \rho^2\ f_{h4}\ f_i\ \eta_0\ \eta_f+2\ C\ \alpha\ \rho^2\ f_{h4}\ f_i\ \eta_0\ \eta_f+$$
$$2\ V\ \alpha\ \rho^2\ f_{h4}\ f_i\ \eta_0\ \eta_f+2\ V\ (1+\rho+\eta_f)-$$
$$2\ (V\ (-1+\rho)+(-V\ (1+\rho)+(-2\ C-V+2\ (C+V)\ \alpha)$$
$$(-(1+\rho)\ f_{h4}+(1+\rho^2)\ (-f_{h3}+f_{h4})\ f_i\ \eta_0))\ \eta_f)\ \eta_p-$$
$$(-2\ C-V+2\ (C+V)\ \alpha)\ (-1+\rho^2)\ (f_{h3}-f_{h4})\ f_i\ \eta_0\ \eta_f\ \eta_p^2-$$
$$C\ f_{h1}\ f_i\ \eta_0\ (1+\rho-(-1+\rho)\ \eta_p)^2+$$
$$C\ f_{h2}\ (-1-\rho+(-1+\rho)\ \eta_p)\ (2+f_i\ \eta_0\ (-1-\rho+(-1+\rho)\ \eta_p))),$$

$$\sigma_{\{h2_{m_1}\}} \to \frac{1}{32}\ (8\ V-C\ f_{h2}\ (2+f_i\ \eta_0\ (-1-\rho+(-1+\rho)\ \eta_p))^2-$$
$$(-2\ C-V+2\ (C+V)\ \alpha)\ f_{h4}\ (2+f_i\ \eta_0\ (-1-\rho+(-1+\rho)\ \eta_p))$$
$$(-2+f_i\ \eta_0\ \eta_f\ (1-\rho+(1+\rho)\ \eta_p))+f_i\ \eta_0\ (C\ f_{h1}$$
$$(-1-\rho+(-1+\rho)\ \eta_p)\ (2+f_i\ \eta_0\ (-1-\rho+(-1+\rho)\ \eta_p))+$$
$$2\ V\ (-1-\rho+(-1+\rho)\ \eta_p-\eta_f\ (1-\rho+(1+\rho)\ \eta_p))+$$
$$(-2\ C-V+2\ (C+V)\ \alpha)\ f_{h3}\ (-1-\rho+(-1+\rho)\ \eta_p)$$
$$(-2+f_i\ \eta_0\ \eta_f\ (1-\rho+(1+\rho)\ \eta_p)))),$$

$$\sigma_{\{h3_{m_1}\}} \to \frac{1}{32}\ f_i\ \eta_0\ (2\ V\ (1+\rho-(-1+\rho)\ \eta_p)-$$
$$C\ (f_{h3}-f_{h4})\ f_i\ \eta_0\ \eta_f^2\ (1-\rho+(1+\rho)\ \eta_p)^2+$$
$$\eta_f\ (1-\rho+(1+\rho)\ \eta_p)\ (2\ V-2\ C\ f_{h4}+$$
$$(-V+2\ (C+V)\ \alpha)\ f_{h1}\ f_i\ \eta_0\ (-1-\rho+(-1+\rho)\ \eta_p))-$$
$$(-V+2\ (C+V)\ \alpha)\ f_{h2}\ (-1-\rho+(-1+\rho)\ \eta_p)$$
$$(-2+f_i\ \eta_0\ \eta_f\ (1-\rho+(1+\rho)\ \eta_p))),\ \sigma_{\{h4_{m_1}\}} \to$$

$$\frac{1}{32}\ (8\ V+(-V+2\ (C+V)\ \alpha)\ f_{h2}\ (2+f_i\ \eta_0\ (-1-\rho+(-1+\rho)\ \eta_p))$$
$$(-2+f_i\ \eta_0\ \eta_f\ (1-\rho+(1+\rho)\ \eta_p))-$$
$$C\ f_{h4}\ (-2+f_i\ \eta_0\ \eta_f\ (1-\rho+(1+\rho)\ \eta_p))^2+$$
$$f_i\ \eta_0\ (-2\ V\ (1+\rho)+2\ V\ (-1+\rho)\ \eta_p+$$
$$C\ f_{h3}\ f_i\ \eta_0\ \eta_f^2\ (1-\rho+(1+\rho)\ \eta_p)^2-$$
$$\eta_f\ (1-\rho+(1+\rho)\ \eta_p)\ (2\ (V+C\ f_{h3})+(-V+2\ (C+V)\ \alpha)$$
$$f_{h1}\ (2+f_i\ \eta_0\ (-1-\rho+(-1+\rho)\ \eta_p)))))),$$

$$\sigma_{\{i_{m_2}\}} \to -\frac{1}{32}\ \eta_0\ (-2\ V\ f_{h3}-2\ V\ \rho\ f_{h3}+2\ V\ f_{h4}+2\ V\ \rho\ f_{h4}+$$
$$4\ \gamma\ f_p+4\ \gamma\ \rho\ f_p-2\ V\ f_{h3}\ \eta_f+2\ V\ \rho\ f_{h3}\ \eta_f+2\ V\ f_{h4}\ \eta_f-$$
$$2\ V\ \rho\ f_{h4}\ \eta_f+2\ C\ f_{h3}\ f_{h4}\ \eta_f-2\ C\ \rho\ f_{h3}\ f_{h4}\ \eta_f-$$

$$2\,C\,f_{h4}^2\,\eta_f + 2\,C\,\rho\,f_{h4}^2\,\eta_f + 4\,\gamma\,f_p\,\eta_f - 4\,\gamma\,\rho\,f_p\,\eta_f +$$
$$C\,f_{h3}^2\,f_i\,\eta_0\,\eta_f^2 - 2\,C\,\rho\,f_{h3}^2\,f_i\,\eta_0\,\eta_f^2 + C\,\rho^2\,f_{h3}^2\,f_i\,\eta_0\,\eta_f^2 -$$
$$2\,C\,f_{h3}\,f_{h4}\,f_i\,\eta_0\,\eta_f^2 + 4\,C\,\rho\,f_{h3}\,f_{h4}\,f_i\,\eta_0\,\eta_f^2 -$$
$$2\,C\,\rho^2\,f_{h3}\,f_{h4}\,f_i\,\eta_0\,\eta_f^2 + C\,f_{h4}^2\,f_i\,\eta_0\,\eta_f^2 - 2\,C\,\rho\,f_{h4}^2\,f_i\,\eta_0\,\eta_f^2 +$$
$$C\,\rho^2\,f_{h4}^2\,f_i\,\eta_0\,\eta_f^2 - 2\,(-(-1+\rho)\,(V\,f_{h3} - V\,f_{h4} - 2\,\gamma\,f_p) +$$
$$(1+\rho)\,((f_{h3} - f_{h4})\,(V - C\,f_{h4}) - 2\,\gamma\,f_p)\,\eta_f +$$
$$C\,(-1+\rho^2)\,(f_{h3} - f_{h4})^2\,f_i\,\eta_0\,\eta_f^2)\,\eta_p +$$
$$C\,(1+\rho)^2\,(f_{h3} - f_{h4})^2\,f_i\,\eta_0\,\eta_f^2\,\eta_p^2 +$$
$$C\,f_{h1}^2\,f_i\,\eta_0\,(1+\rho-(-1+\rho)\,\eta_p)^2 +$$
$$C\,f_{h2}^2\,(-1-\rho+(-1+\rho)\,\eta_p)\,(2+f_i\,\eta_0\,(-1-\rho+(-1+\rho)\,\eta_p)) -$$
$$2\,f_{h1}\,(V\,(1+\rho-(-1+\rho)\,\eta_p) + C\,f_{h2}\,(-1-\rho+(-1+\rho)\,\eta_p)$$
$$(1+f_i\,\eta_0\,(-1-\rho+(-1+\rho)\,\eta_p)) - \eta_f\,(1-\rho+(1+\rho)\,\eta_p)$$
$$(-V + C\,f_{h3}\,f_i\,\eta_0\,(1+\rho+\eta_p-\rho\,\eta_p) + f_{h4}\,(2\,C+V-$$
$$2\,(C+V)\,\alpha + C\,f_i\,\eta_0\,(-1-\rho+(-1+\rho)\,\eta_p)))) -$$
$$2\,f_{h2}\,(-V\,(1+\rho+\eta_p-\rho\,\eta_p+\eta_f\,(1-\rho+(1+\rho)\,\eta_p)) -$$
$$f_{h3}\,(-1-\rho+(-1+\rho)\,\eta_p)$$
$$(V - 2\,(C+V)\,\alpha + C\,f_i\,\eta_0\,\eta_f\,(1-\rho+(1+\rho)\,\eta_p)) +$$
$$f_{h4}\,(-(-V+2\,(C+V)\,\alpha)\,(-1-\rho+(-1+\rho)\,\eta_p) +$$
$$\eta_f\,(1-\rho+(1+\rho)\,\eta_p)\,(2\,C+V-2\,(C+V)\,\alpha +$$
$$C\,f_i\,\eta_0\,(-1-\rho+(-1+\rho)\,\eta_p)))))\Big\}$$

4 - Quasi-linkage-equilibrium analysis

When selection is weak relative to recombination, alleles will be only weakly associated with each other. Accordingly, the values of the genetical associations are of the same order of magnitude as the selection coefficients. After a few generations of selection and recombination, the associations converge on quasi-equilibrium values that change slowly as the allele frequencies evolve. We now calculate the quasi-equilibrium values for the associations, and will substitute these into the equations that describe the change of allele frequencies in the final section of this appendix.

■ Quasi-Linkage equilibrium values for the associations

We are now ready to calculate quasi-linkage-equilibrium values for all the associations that are needed. For example, the QLE value of $\tilde{D}[\{i, p\}]$ can be solved from

```
eqip = eqQLE[{i, p}] == 0
```

$$\epsilon\left(\frac{1}{4}\,(f_i - f_i^2)\,(f_p - f_p^2)\,\sigma_{\{i_{m_1}, p_f\}} - \frac{1}{2}\,\tilde{D}[\{i, p\}]\right) == 0$$

After defining similar equations for the other association, we find the following quasi-linkage-equilibrium values

$$\Big\{\tilde{D}[\{i, p\}] \to \frac{1}{2}\,(-1+f_i)\,f_i\,(-1+f_p)\,f_p\,\sigma_{\{i_{m_1}, p_f\}},$$
$$\tilde{D}[\{h1, p\}] \to \frac{1}{2}\,(-1+f_{h1})\,f_{h1}\,(-1+f_p)\,f_p\,\sigma_{\{h1_{m_1}, p_f\}},$$

$$\tilde{D}[\{h2, p\}] \to \frac{1}{2}\,(-1+f_{h2})\,f_{h2}\,(-1+f_p)\,f_p\,\tilde{\sigma}_{\{h2_{m_1},p_f\}},$$
$$\tilde{D}[\{h3, p\}] \to \frac{1}{2}\,(-1+f_{h3})\,f_{h3}\,(-1+f_p)\,f_p\,\tilde{\sigma}_{\{h3_{m_1},p_f\}},$$
$$\tilde{D}[\{h4, p\}] \to \frac{1}{2}\,(-1+f_{h4})\,f_{h4}\,(-1+f_p)\,f_p\,\tilde{\sigma}_{\{h4_{m_1},p_f\}},$$
$$\tilde{D}[\{h1, h2, p\}] \to 0,\ \tilde{D}[\{h1, h3, p\}] \to 0,$$
$$\tilde{D}[\{h1, h4, p\}] \to 0,\ \tilde{D}[\{h2, h3, p\}] \to 0,$$
$$\tilde{D}[\{h2, h4, p\}] \to 0,\ \tilde{D}[\{h3, h4, p\}] \to 0,\ \tilde{D}[\{h1, i, p\}] \to 0,$$
$$\tilde{D}[\{h2, i, p\}] \to 0,\ \tilde{D}[\{h3, i, p\}] \to 0,\ \tilde{D}[\{h4, i, p\}] \to 0\Big\}$$

■ Equations for allele frequency change

The final step of the analysis is to derive equations for the change of allele frequencies from one generation to the next.

The equations for the male characters are calculated up to first order in ϵ.

```
Δi = eqFreq[i, 1] /. selCoeffSimpl
```

$$-\frac{1}{2}\,\epsilon\,(-1+f_i)\,f_i\,(\tilde{\sigma}_{\{i_{m_1}\}}+\tilde{\tau}_{\{i\}})$$

```
Δh1 = eqFreq[h1, 1]
```

$$-\frac{1}{2}\,\epsilon\,(-1+f_{h1})\,f_{h1}\,\tilde{\sigma}_{\{h1_{m_1}\}}$$

```
Δh2 = eqFreq[h2, 1]
```

$$-\frac{1}{2}\,\epsilon\,(-1+f_{h2})\,f_{h2}\,\tilde{\sigma}_{\{h2_{m_1}\}}$$

```
Δh3 = eqFreq[h3, 1]
```

$$-\frac{1}{2}\,\epsilon\,(-1+f_{h3})\,f_{h3}\,\tilde{\sigma}_{\{h3_{m_1}\}}$$

```
Δh4 = eqFreq[h4, 1]
```

$$-\frac{1}{2}\,\epsilon\,(-1+f_{h4})\,f_{h4}\,\tilde{\sigma}_{\{h4_{m_1}\}}$$

The equation for the dynamics of the female preference allele is given up to second order in ϵ, since all first order terms vanish, i.e., selection on the female mating preference is weak. At quasi-linkage equilibrium,

```
Δp = eqFreq[p, 2] /. DuQle /. selCoeffSimpl // FullSimplify
```

$$\frac{1}{4}\,\epsilon^2\,(-1+f_p)\,f_p$$
$$(-2\,\hat{\sigma}_{\{p_f\}}+(-1+f_i)\,f_i\,\tilde{\sigma}_{\{i_{m_1},p_f\}}\,(\tilde{\sigma}_{\{i_{m_1}\}}+\tilde{\tau}_{\{i\}})-2\,\tilde{\omega}_{\{p\}})$$

Appendix 7.2
The asymmetric Hawk-Dove game

Local payoffs:
The expected payoff of an individual with strategy p (= probability to play Hawk) in a contest with an opponent with strategy q is given by:

$$f_x(p|q) = pg\cdot((1/2+x)V-(1/2-x)C)+p(1-q)\cdot V+(1-p)(1-q)\cdot 1/2\,V, \qquad (7)$$

where $1/2+x$ $(-1/2 \le x \le 1/2)$ is the probability that the focal individual wins a Hawk-Hawk confrontation. In our model, x can take on the values $+\alpha$,$-\alpha$ and 0. Simplification of the local payoff function yields

$$f_x(p|q) = 1/2V\cdot(1+p-q) - 1/2\,Cpq+(V+C)xpq\,. \qquad (8)$$

Accordingly, the local selection gradient is given by:

$$\frac{\partial f_x}{\partial p}(p|q) = 1/2V - 1/2\,Cq+(V+C)xq\,. \qquad (9)$$

It will be useful to rewrite this gradient in terms of $v = V/C$, which corresponds to the ESS in the classical Hawk-Dove game without fighting asymmetries. In fact, up to the factor $1/2C$ (which will henceforth be neglected, since it does not affect the analysis in any way), the local selection gradient is of the form:

$$\frac{\partial f_x}{\partial p}(p|q) = v-q+2x(1+v)q\,. \qquad (10)$$

Non-signalling equilibria:
Let us assume that there are two types of individuals in the population (indicated by '+' and '–') that differ in fighting ability. In confrontations of two individuals differing in fighting ability, the +-type wins a Hawk-Hawk confrontation with probability $1/2+\alpha$, while the other individual wins with probability $1/2-\alpha$. Individuals know their own fighting ability, but they do not signal it to their opponents. Accordingly, individual strategies are only conditional on their own type: $\mathbf{p} = (p_+,p_-)$. Let $\hat{\mathbf{p}} = (\hat{p}_+,p_-)$ denote the population strategy. Then the expected payoff of an individual of type + resp. – is given by:

$$\begin{aligned} F_+(\mathbf{p}|\hat{\mathbf{p}}) &= 1/2\,f_0(p_+|\hat{p}_+)+1/2\,f_\alpha(p_+|\hat{p}_-) \\ F_-(\mathbf{p}|\hat{\mathbf{p}}) &= 1/2\,f_{-\alpha}(p_-|\hat{p}_+)+1/2\,f_0(p_-|\hat{p}_-) \end{aligned}\,. \qquad (11)$$

In view of (9), the selection gradients in both situations are given by:

$$\begin{aligned}\frac{\partial F_+}{\partial p_+}(\mathbf{p}|\hat{\mathbf{p}}) &= v - \tfrac{1}{2}(\hat{p}_+ + \hat{p}_-) + \alpha(1+v)\hat{p}_- \\ \frac{\partial F_-}{\partial p_-}(\mathbf{p}|\hat{\mathbf{p}}) &= v - \tfrac{1}{2}(\hat{p}_+ + \hat{p}_-) - \alpha(1+v)\hat{p}_+\end{aligned} \quad . \tag{12}$$

Every Nash strategy $\hat{p}_i$ (where $i \in \{+,-\}$) has to satisfy the following condition:

$$\frac{\partial F_i}{\partial p_i}(\mathbf{p}|\hat{\mathbf{p}}) \quad \begin{cases} \leq 0 & \text{if } \hat{p}_i = 0 \\ = 0 & \text{if } 0 < \hat{p}_i < 1 \\ \geq 0 & \text{if } \hat{p}_i = 1 \end{cases} . \tag{13}$$

For the special case $\alpha = 0$, (12) immediately implies that the asymmetric Hawk-Dove game has a line of equilibria that is given by $\frac{1}{2}(\hat{p}_+ + \hat{p}_-) = v$, which correspond to the (single) equilibrium of the classical Hawk-Dove game without differences in fighting ability. Let us from now on assume that $\alpha > 0$.
Notice that (12) implies:

$$\frac{\partial F_+}{\partial p_+}(\mathbf{p}|\hat{\mathbf{p}}) > \frac{\partial F_-}{\partial p_-}(\mathbf{p}|\hat{\mathbf{p}}) , \tag{14}$$

unless $\hat{p}_+ = \hat{p}_- = 0$. The latter possibility can be neglected, since it is obvious from (12) that $(\hat{p}_+,\hat{p}_-) = (0,0)$ is not a Nash equilibrium. From (14) we can conclude that there is no fully mixed Nash equilibrium, i.e. no Nash equilibrium with $0 < \hat{p}_+, \hat{p}_- < 1$. At such an equilibrium, both selection gradients in (12) would have to be zero and, hence, to be identical, which is precluded by (14). It is also obvious from (12) that $(\hat{p}_+,\hat{p}_-) = (1,1)$ is no Nash equilibrium. Combining (13) and (14) we can therefore conclude that there are three possible types of Nash equilibria: (a) $\hat{p}_- = 0$ and $0 < \hat{p}_+ < 1$; (b) $p_+ = 1$ and $0 < \hat{p}_- < 1$; or (c) $(\hat{p}_+,\hat{p}_-) = (1,0)$.
Let us first consider the equilibria of type (a). The selection gradient for $\hat{p}_+$ has to satisfy

$$\frac{\partial F_+}{\partial p_+}(\mathbf{p}|\hat{\mathbf{p}}) = v - \tfrac{1}{2}\,\hat{p}_+ = 0 , \tag{15}$$

yielding $\hat{p}_+ = 2v$. This requires $v \leq \frac{1}{2}$. In this case, $(\hat{p}_+,\hat{p}_-) = (2v,0)$ is indeed a Nash equilibrium, since (14) implies $\partial F_-/\partial p_- \leq 0$
Next consider the equilibria of type (b). The selection gradient for $\hat{p}_-$ has to satisfy

$$\frac{\partial F_-}{\partial p_-}(\mathbf{p}|\hat{\mathbf{p}}) = v - \tfrac{1}{2}(1 + \hat{p}_-) - \alpha\,(1+v) = 0 , \tag{16}$$

yielding $\hat{p}_- = 2(1-\alpha)v-(1+2\alpha)$. This requires $v \geq (\alpha+1/2)/(1-\alpha)$. If this is the case, $(\hat{p}_+,\hat{p}_-)$ is indeed a Nash equilibrium, since (14) implies $\partial F_+/\partial p_+ \geq 0$.

Let us finally consider the pure-strategy equilibrium $(\hat{p}_+,\hat{p}_-)=(1,0)$. A simple calculation shows that the requirement $\partial F_+/\partial p_+ \geq 0 \geq \partial F_-/\partial p_-$ is satisfied for $1/2 \leq v \leq (\alpha+1/2)/(1-\alpha)$.

Taking all this together, we obtain the following (unique) Nash equilibrium in the non-signalling context (see figure 7.2A in the main text):

$$\begin{aligned}
&\hat{p}_-=0 \text{ and } \hat{p}_+=2v && \text{if } \ v \leq 1/2 \\
&\hat{p}_-=0 \text{ and } \hat{p}_+=1 && \text{if } \ 1/2 \leq v \leq (\alpha+1/2)/(1-\alpha)\ . \qquad (17)\\
&\hat{p}_-=2(1-\alpha)v-(1+2\alpha) \text{ and } \hat{p}_+=1 && \text{if } \ (\alpha+1/2)/(1-\alpha) \leq v
\end{aligned}$$

Notice that $1/2(\hat{p}_++\hat{p}_-)= v$ only holds for the equilibria of type (a) (i.e. if $v \leq 1/2$). For the other equilibria, the average tendency to play Hawk is smaller than in the classical Hawk-Dove game without fighting asymmetries.

Signalling equilibria:
Let us now consider the situation where all individuals invest into the ornament. All individu-als with high fighting ability develop the ornament, while individuals with low fighting ability develop the ornament with probability η. Individual strategies are now dependent on own fighting ability (+ or –) and the presence or absence (1 or 0) of the ornament in the opponent: $\mathbf{p} = (p_{+1},p_{+0},p_{-1},p_{-0})$. Again $\hat{\mathbf{p}} = (\hat{p}_{+1},\hat{p}_{+0},\hat{p}_{-1},\hat{p}_{-0})$ denotes the population strategy.

A focal individual matched with an opponent without ornament 'knows' that the opponent has low fighting ability. If it is matched with an ornamented opponent, the probability that the opponent has high (resp. low) fighting ability is $1/(1+\eta)$ (resp. $\eta/(1+\eta)$). If the focal indi-vidual has high fighting ability, its opponent will always perceive the ornament; if it has low fighting ability, the opponent will perceive the ornament with probability . Based on these considerations, one can calculate the expected payoff of a $\mathbf{p}$–individual in a $\hat{\mathbf{p}}$–population for each of the four information situations:

$$\begin{aligned}
F_{+0}(\mathbf{p}|\hat{\mathbf{p}}) &= f_\alpha(p_{+0}\,|\,\hat{p}_{-1}) \\
F_{+1}(\mathbf{p}|\hat{\mathbf{p}}) &= 1/(1+\eta)\, f_0(p_{+1}\,|\,\hat{p}_{+1}) + \eta/(1+\eta)\, f_\alpha(p_{+1}\,|\,\hat{p}_{-1}) \\
F_{-0}(\mathbf{p}|\hat{\mathbf{p}}) &= \eta\, f_0(p_{-0}\,|\,\hat{p}_{-1}) + (1-\eta)\, f_0(p_{-0}\,|\,\hat{p}_{-0}) \\
F_{-1}(\mathbf{p}|\hat{\mathbf{p}}) &= \eta(1/(1+\eta)\, f_{-\alpha}(p_{-1}\,|\,\hat{p}_{+1}) + \eta/(1+\eta)\, f_0(p_{-1}\,|\,\hat{p}_{-1})) + \\
&\quad (1-\eta)(1/(1+\eta)\, f_{-\alpha}(p_{-1}\,|\,\hat{p}_{+0}) + \eta/(1+\eta)\, f_0(p_{-1}\,|\,\hat{p}_{-0}))\ . \qquad (18)
\end{aligned}$$

In view of (10), the selection gradients in the four information situations are given by:

$$\frac{\partial F_{+0}}{\partial p_{+0}} = v - \hat{p}_{-1} + 2\alpha(1+v)\hat{p}_{-1} \tag{19}$$

$$\frac{\partial F_{+1}}{\partial p_{+1}} = v - (1/(1+\eta)\ \hat{p}_{+1} + \eta/(1+\eta)\ \hat{p}_{-1}) + 2\alpha(1+v)\eta/(1+\eta)\ \hat{p}_{-1}$$

$$\frac{\partial F_{-0}}{\partial p_{-0}} = v - (\eta\hat{p}_{-1} + (1-\eta)\hat{p}_{-0})$$

$$\frac{\partial F_{-1}}{\partial p_{-1}} = v - \big(\eta/(1+\eta)\ \hat{p}_{+1} + \eta^2/(1+\eta)\ \hat{p}_{-1} + (1-\eta)/(1+\eta)\ \hat{p}_{+0} + \eta(1-\eta)/(1+\eta)\hat{p}_{-0}\big) - 2\alpha(1+v)\cdot\big(\eta/(1+\eta)\ \hat{p}_{+1} + (1-\eta)/(1+\eta)\ \hat{p}_{+0}\big)\ .$$

In the absence of fighting asymmetries (i.e. $\alpha = 0$) the unique Nash equilibrium is given by $\hat{p}_{+1} = \hat{p}_{+0} = \hat{p}_{-1} = \hat{p}_{-0} = v$. In other words: the ESS of the Hawk-Dove game without fighting asymmetries is played in all information situations. More generally, there exists a completely mixed Nash equilibrium if (and only if) the fighting asymmetry α is sufficiently small. In fact, all selection gradients in (19) are equal to zero if $\hat{\mathbf{p}}$ is given by:

$$\hat{p}_{+1} = v,\ \hat{p}_{-1} = \frac{v}{1-2\alpha(1+v)},\ \hat{p}_{+0} = \frac{1-\eta-2\alpha\eta(1+v)}{1-\eta}\cdot\hat{p}_{-1},$$
$$\hat{p}_{-0} = \frac{1-\eta-2\alpha(1+v)}{1-\eta}\cdot\hat{p}_{-1}. \tag{20}$$

and the strategic parameters in (20) are between zero and one if α satisfies the inequality

$$\alpha \leq \tfrac{1}{2}\cdot\min\left\{\frac{1-v}{1+v}\ ,\ \frac{1-\eta}{1+v}\right\}\ . \tag{21}$$

Notice that the equilibrium in (20) is 'paradoxical' in that $\hat{p}_{-1}$ is larger than all the other strategic parameters. In other words, an individual with low fighting ability that is confronted with an ornamented (and, hence, potentially strong) opponent is more inclined to play the Hawk strategy than, say an individual with high fighting ability that is confronted with a non-ornamented opponent (which definitely has low fighting ability). For small values of α, there exist even more extreme paradoxical equilibria. In particular,

$$\hat{p}_{-1} = 1,\ \hat{p}_{+1} = \hat{p}_{+0} = \hat{p}_{-0} = 0 \tag{22}$$

is a pure-strategy Nash equilibrium if

$$\alpha \le \tfrac{1}{2} \cdot \frac{1-\nu-\nu/\eta}{1+\nu} \quad \text{and} \quad \frac{\eta}{1+\eta} > \nu > \frac{\eta^2}{1+\eta} . \tag{23}$$

Let us from now on focus on the 'common-sense' equilibria, where $\hat{p}_{-1}$ is small. If we assume $\hat{p}_{-1}=0$, the selection gradient for p_{+0} is positive, implying that $\hat{p}_{+0}=1$ at equilibrium. In other words, individuals with low fighting ability that are confronted with an ornamented opponent always play Dove, while individuals with high fighting ability that are confronted with a non-ornamented opponent always play Hawk. The selection gradient for p_{+1} (resp. p_{-0}) is positive at $\hat{p}_{+0}=0$ (resp. at $\hat{p}_{-0}=0$). This implies that both strategies have to be positive at equilibrium. The selection gradient for p_{+1} (resp. p_{-0}) is equal to zero for $\hat{p}_{+1}=(1+\eta)\nu$ (resp. $\hat{p}_{-0}=\nu/(1-\eta)$). Nash equilibria with $\hat{p}_{-1}=0$ therefore have to satisfy:

$$\hat{p}_{-1}=0,\ \hat{p}_{+0}=1, \text{ and } \begin{cases} \hat{p}_{+1}=(1+\eta)\cdot\nu \text{ and } \hat{p}_{-0}=\nu/(1-\eta) & \text{if } \nu \le 1-\eta \\ \hat{p}_{+1}=(1+\eta)\cdot\nu \text{ and } \hat{p}_{-0}=1 & \text{if } 1-\eta \le \nu \le 1/(1-\eta) \\ \hat{p}_{+1}=\ \hat{p}_{-0}=1 & \text{if } 1/(1-\eta) \le \nu \end{cases} . \tag{24}$$

Notice that in all cases $\hat{p}_{+1} \le \hat{p}_{-0}$.The strategy combination given by (24) is indeed a Nash equilibrium if the selection gradient for p_{-1} is negative or zero at $\hat{p}_{-1}=0$. This is the case for

$$\nu \le \Psi = \frac{1+\eta\,(1-\eta)+2\alpha}{1+\eta-2\alpha} . \tag{25}$$

In other words, (24) does indeed give a Nash equilibrium if $\nu \le \Psi$. Notice that $\Psi > 1/(1+\eta)$, i.e. (24) potentially loses the equilibrium property in situations where $\hat{p}_{+0}=\hat{p}_{+1}=\hat{p}_{-0}=1$. In this case the equilibrium is given by:

$$\hat{p}_{+0}=\hat{p}_{+1}=\hat{p}_{-0}=1 \text{ and } \hat{p}_{-1}=1-\frac{1}{\eta^2}\cdot\big((1+\eta)(1-\nu)+2\alpha(1+\nu)\big) . \tag{26}$$

The 'common-sense' equilibria characterized by (24) and (26) are illustrated by Figure 7.2B in the main text.